2001

The Non-Indigenous Ant, Solenopsis invicta, Reduces Loggerhead Shrike and Native Insect Abundance

Craig R. Allen
Clemson University, callen3@unl.edu

R. Scott Lutz
University of Wisconsin

Tim Lockley
U.S. Department of Agriculture

Sherman A. Phillips Jr.
Texas Tech University

Stephen Demarais
Mississippi State University, steve.demarais@msstate.edu

The Non-Indigenous Ant, *Solenopsis invicta*, Reduces Loggerhead Shrike and Native Insect Abundance[1]

Craig R. Allen, R. Scott Lutz,[2] Tim Lockley,[3] Sherman A. Phillips, Jr.,[4] and Stephen Demarais[5]

U.S. Geological Survey, Biological Resources Division, South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson, South Carolina 29634

J. Agric. Urban Entomol. 18(4): 249–259 (October 2001)

ABSTRACT The red imported fire ant (*Solenopsis invicta* Buren) is an aggressive, non-indigenous species that is a threat to native biota in the southeastern United States. We determined the effect of *S. invicta* on loggerhead shrike (*Lanius ludovicianus* L.) abundance and investigated a possible mechanism of impact, which is a reduction in insect prey availability. We used a fire ant bait (hydramethylnon) to reduce fire ant populations on one randomly chosen member of each of five pairs of 202-ha study areas in the Texas coastal Bend region, and also measured shrike relative abundance and a volumetric index of insect biomass on the study areas. Loggerhead shrike relative abundance was assessed at five counting stations established along 3.2-km transects through prairie habitat on each study area during the fall of 1992 and 1993. We sampled non-*S. invicta* invertebrates with 13.3-L capacity UV light traps and found that insect volume, species richness, and diversity were greater on treated sites. More shrikes were observed on areas where *S. invicta* populations had been reduced. Both insect biomass and shrike abundance were negatively correlated to the level of *S. invicta* infestation. Our data suggest that shrikes may avoid areas on wintering habitats that have been invaded by *S. invicta* and that this avoidance may result from reduced insect availability.

KEY WORDS endangered species, Formicidae, Hymenoptera, invasive species, Laniidae, *Lanius ludovicianus*, Passeriformes

Ants are important in ecological systems, acting as keystone species in many instances (Risch & Carroll 1982). Ants provide key and irreplaceable ecosystem services such as pollination, nutrient turnover, energy flow, and seed dispersal (Handel et al. 1981). As invasive or introduced species, ants also may have a large impact by affecting native invertebrate (Porter & Savignano 1990, Cole et al.

[1]Accepted for publication 12 March 2002.
[2]Department of Wildlife Ecology, 1630 Linden Drive, 226 Russell Labs, University of Wisconsin, Madison, Wisconsin 53706.
[3]U.S. Department of Agriculture, APHIS, PPQ, Imported Fire Ant Station, 3505 25th Avenue, Gulfport, Mississippi 39501.
[4]Department of Plant and Soil Sciences, Texas Tech University, Lubbock, Texas 79409.
[5]Department of Wildlife and Fisheries, Mississippi State University, Mississippi State, Mississippi 39762.

1992) and vertebrate species (Allen et al. 1998), as well as ecological processes (Bond & Slingsby 1984, Zettler et al. 2001).

The red imported fire ant (*Solenopsis invicta* Buren) is native to the Pantanal flood plain of South America and was introduced into the United States in the vicinity of Mobile, Alabama, in the 1930s (Vinson & Sorensen 1986). It spread throughout the southeastern United States and continues to expand its range and populations at both local (Wojcik 1994) and regional scales (Cokendolpher & Phillips 1989). *S. invicta* is of interest to ecologists and invasion biologists because of its rapid spread and increasing evidence of negative impacts on diverse native fauna, both vertebrate and invertebrate.

In its native range, and historically in the United States, *S. invicta* are predominately monogynous, with a single fertile queen in each colony, and are intraspecifically territorial. Polygyny was unknown in *S. invicta* until the discovery of multiple-queen colonies in Mississippi (Glancey et al. 1973). Competition among monogynous colonies generally maintains colony densities at <99/ha (Wojcik 1983). Polygynous colonies are characterized by high mound densities (>100 mounds/ha) associated with an apparent failure of the nest-mate recognition system and subsequent loss of territoriality (Mirenda & Vinson 1982). Polygynous colonies are now common in some infested regions, most notably in Texas where >50% of all colonies are polygynous (Porter et al. 1991). The sustained high population densities associated with polygyne *S. invicta* have increased the potential for negative impacts on native invertebrate and vertebrate species and communities.

Impacts on vertebrates, and in particular on avian species, include decreased fledgling success (Sikes & Arnold 1986) and population reductions (Allen et al. 1995). *S. invicta* may prey on pipping young (Allen et al. 1994, Drees 1994) and have indirect impacts on behavior (Pedersen et al. 1996), survival, and weight gain (Guiliano et al. 1996, Allen et al. 1997). Presumably, decreases in insects such as orthopterans and lepidopteran larvae and overall decreases in arthropod abundance (Porter & Savignano 1990) have indirect negative influences on insectivorous birds (and other animals) by decreasing food availability.

Loggerhead shrikes (*Lanius ludovicianus* L.) and *S. invicta* forage on many of the same insect species, and shrike-cached insects may be consumed by *S. invicta*. We hypothesized that fire ants may reduce insect availability for wintering shrikes, thereby reducing habitat quality for shrikes on wintering grounds. To test this hypothesis, we reduced fire ant populations and measured the effect on a volumetric index of available invertebrate biomass and loggerhead shrike relative abundance.

Materials and Methods

We conducted our research on three private ranches in the Texas Coastal Prairie vegetational area of Texas (Gould, 1975). We selected 10 202-ha study areas (five pairs: R1, R2, V1, VC1, and VC2) during the fall of 1990 and paired them based on similarities in degree of *S. invicta* infestation, vegetation, soils, and pretreatment wildlife indices. A detailed description of the study areas appears in Allen et al. (1995).

Red imported fire ant populations were reduced on one randomly chosen member of each study area pair with aerial applications (1.67 kg/ha) of Hydramethylnon (Amdro®) fire ant bait (American Cyanamid Co., Wayne, New Jersey), a

delayed-action toxicant. Hydramethylnon was applied in April and October 1991, and May 1992. Fire ant populations and the efficacy *of S. invicta* population reductions were assessed with 10 0.10-ha, non-overlapping circle counts near the center of each study area. All *S. invicta* mounds within each 0.10-ha circle were counted and assigned a value corresponding to mound size and presence or absence of worker brood (Lofgren & Williams 1982). This index weights colonies with worker brood more heavily than colonies without, because the lack of worker brood indicates the absence of a fertile queen and, thus, a moribund colony. Red imported fire ants were surveyed prior to treatments (April 1991) and seven times post-treatment. Efficacy of treatments to reduce *S. invicta* populations were analyzed with randomized design block analysis of variance using pretreatment fire ant indices as a covariate (Allen et al. 1995).

Six of the 10 available 202-ha study areas in three pairs (R1, V1, and VC1; Allen et al. 1995) were used to investigate *S. invicta* impact on invertebrate biomass measured indirectly via collected volume. We sampled (non-*S. invicta*) invertebrates with 13.3-L capacity UV light traps (Universal Black Light Trap 2851A, BioQuip Products, Gardena, California) using one trap-night per study area during each sampling period. Light traps were placed at ground level >100 m from study area boundaries approximately 30 min before sunset, and they were collected and emptied approximately 30 min after sunrise. Placement of traps on the ground and well within study area boundaries on our brush-prairie sites limited visibility so that our sampling was restricted as much as possible to invertebrates residing in our study areas. Members of a study area pair were sampled concurrently during three nights of consecutive sampling. The contents of light traps were transferred to graduated cylinders and were settled by tapping prior to the measurement of volume. Recovered Carabidae, Scarabidae, orthopterans (Tettigoniidae, Acrididae, Tetrigidae, Gryllotalpidae, and Gryllidae), and Dictyoptera (roaches) were identified to species. We compared species richness and diversity using the Shannon Diversity Index (Magurran 1988) among treated and untreated sites with Wilcoxon signed rank tests because the data were not normally distributed ($P < 0.04$). Data from light traps (cm^3 of insects per study area) were analyzed with randomized block design analysis of variance (SAS Institute 1989). Each sampling period was analyzed separately because species turnover was high between sampling periods and thus represented independent samples. Voucher specimens are maintained at the U.S. Department of Agriculture Imported Fire Ant Station (Gulfport, Mississippi).

Pretreatment data were collected in April 1991, and treatment data were collected in June, July, and October 1991, and again in January (*S. invicta* indices only), March, May (biomass only), June, August, and October (biomass only) of 1992. In June and August 1993, sampling documented *S. invicta* populations and insect biomass >1 year after the cessation of treatments. Pearson correlation analysis was used to test for a relationship between *S. invicta* indices and insect biomass for those periods where both measurements were collected. To decrease the chance of Type II error, we considered $P < 0.10$ significant (Tacha et al. 1982).

We measured loggerhead shrike relative abundance on 3.2-km transects (Allen et al. 1995) through representative habitat on each study area. Five regularly spaced counting stations were placed on each transect. Transects were walked within 3 h of sunrise/sunset, and 3 min were spent at each station counting all shrikes seen within 50 m of the station. Stations were surveyed 12 times on each

study area between 2 September and 2 November 1992 for a total of 60 counts on each study area. Between 1 September and 13 November 1993, stations were surveyed an average of 17 times (range 13–26) for a total of 85 counts on each study area. Members of paired study areas were counted simultaneously. Shrike abundance was expressed as the average number of shrikes observed on each five-station transect. Loggerhead shrike abundance was analyzed with randomized block design analysis of variance, and we calculated both linear and nonlinear regressions to determine if shrike abundance was affected by fire ant abundance as measured by indices (SAS Institute 1989).

Results

Fire ants in our study areas were primarily polygynous (Allen et al. 1995). Prior to treatment, *S. invicta* indices averaged 435 per 0.10-ha plot on treated areas and 297 per 0.10-ha plot on untreated areas, roughly corresponding to average mound densities of 290 and 198 mounds/ha, respectively. Following treatments, *S. invicta* population indices were reduced on treated sites (see Allen et al. 1995), remaining below untreated indices for the remainder of 1991 and throughout 1992. *S. invicta* indices after treatment averaged 18% of pretreatment levels on treated sites, whereas they remained virtually unchanged on untreated sites (averaging 105% of pretreatment level). In August 1992, immediately prior to the collection of shrike data, fire ant population levels on treated areas averaged 10% of untreated area indices. In 1993, a year after the last treatment to reduce fire ants, fire ant populations were similar on treated and untreated study areas (Allen et al. 1995).

Before treatments, insect volume was less ($P = 0.08$) on those areas randomly selected to be treated than on untreated areas (Table 1). After treatments, recovered insect volume was greater on treated sites and averaged more than double that of untreated areas. Significant differences were detected in June ($P = 0.02$) and October 1991 ($P = 0.03$) and May 1992 ($P < 0.10$), and approached significance in March ($P = 0.15$) and June 1992 ($P = 0.16$, Table 1). In August 1992, immediately prior to the collection of shrike data, insect volume on untreated sites was 43% of the volume recovered on treated sites. Invertebrate taxa recovered from light traps were predominately Scarabaeidae, Trogidae, Carabidae, Tettigoniidae, Acrididae, and Gryllidae, as well as Lepidoptera, Homoptera, and Hemiptera. A significant negative correlation existed between *S. invicta* indices and recovered invertebrate volume ($r^2 = -0.281$, df = 12, $P = 0.07$). One year after the cessation of treatments, recovered insect volume from treated and untreated areas were similar and not significantly different ($P > 0.10$, Table 1).

Scarabidae, Carabidae, Orthoptera (Tettigoniidae, Acrididae, Tetrigidae, Gryllotalpidae, and Gryllidae), and Dictyoptera were identified to species. Species richness was higher on treated sites ($W = 17$, df = 7, $P = 0.094$; Table 2). One hundred forty-four species were collected, 124 from treated sites and 100 from untreated sites (Table 2). The median Shannon Diversity index for treated sites (1.577) was greater than median diversity (1.386) on untreated sites ($W = 19$, df = 5, $P = 0.063$; Table 2).

We observed 57 shrikes during 600 3-min observation periods. Significantly more shrikes were observed on areas where *S. invicta* populations had been

Table 1. Insect volume (cc) (± one SE) collected from light traps on three pairs of treated and untreated study areas in the Texas Coastal Prairie, 1991–1992.

Date	Treated X ± SE	Untreated X ± SE	*F* value[a]	*P* level
Pretreatment (April 1991)	164 ± 18	248 ± 39	10.5	0.083
June 1991	2,405 ± 244	960 ± 215	60.1	0.016
July	487 ± 105	323 ± 87	3.2	0.213
October	43 ± 3	21 ± 6	33.8	0.028
March 1992	9 ± 4	4 ± 2	5.2	0.151
May	162 ± 90	126 ± 81	8.9	0.096
June	1,007 ± 314	467 ± 91	4.6	0.164
August	670 ± 371	290 ± 98	1.8	0.316
October	135 ± 87	87 ± 57	2.4	0.259
S. invicta recovery period				
June 1993	170 ± 98	177 ± 111	0.3	0.662
August	246 ± 47	8 ± 70	3.1	0.220

[a]2 degrees of freedom in all comparisons.

reduced ($F = 11.58$, df = 4, $P = 0.027$; Table 3). An average of 0.72 shrikes per five-station transect was observed on treated areas, and an average of 0.25 per five-station transect on untreated areas. Linear regressions of the relationship between fall shrike abundance and the abundance of *S. invicta* were significant as measured in both June ($r^2 = 0.650$, df = 9, $P < 0.005$) and August ($r^2 = 0.394$, df = 9, $P < 0.052$; Fig. 1) 1992. However, non-linear models provided a better fit,

Table 2. Species richness (totals) and diversity (means; Shannon Diversity Index) of selected invertebrate families captured in light traps on three pairs of treated and untreated study areas in the Texas Coastal Prairie, 1991–1992.

	Treated		Untreated	
	Richness	Diversity	Richness	Diversity
Carabidae	52	2.886	52	2.963
Tettigoniidae	12	1.367	11	1.107
Acrididae	14	1.832	9	1.665
Tetrigidae	0	–	1	–
Gryllidae	3	0.489	3	0.303
Gryllotalpidae	1	–	0	–
Dictyoptera	3	0.902	1	0
Scarabeidae	39	1.786	23	1.671
Totals or means	124	1.544	100	1.285

Table 3. Loggerhead shrike abundance (± one SE) on five pairs of treated and untreated study areas in the Texas Coastal Prairie, 2 September–2 November 1992.

Study area pair	Treated	Untreated
R1	0.92 ± 0.31	0.08 ± 0.08
R2	0.83 ± 0.21	0.75 ± 0.22
V1	0.67 ± 0.43	0.17 ± 0.17
VC1	0.42 ± 0.15	0.17 ± 0.11
VC2	0.75 ± 0.25	0.08 ± 0.08
Mean ± SE	0.72 ± 0.09	0.25 ± 0.13

explaining more variance (June $r^2 = 0.823$, df = 9, $P = 0.011$, rational four-parameter model; June $r^2 = 0.71$, df = 9, $P = 0.0124$, inverse 2nd order polynomial; Fig. 2). In 1993, less than 1 year after the cessation of treatments to reduce fire ants, shrike populations were similar on treated and untreated study areas ($W = 5$, df = 4, $P = .625$; Table 4).

Discussion

We quantified an increase in overall non-*S. invicta* invertebrate volume, richness, and diversity on areas treated to reduce *S. invicta* populations. Treatments were unlikely to have any direct effect on non-*S. invicta* insects (Apperson et al. 1984). *S. invicta* dominates baits and, even at relatively low density, are the first species to recruit to >95% of baits and to eventually exploit 100% of baits (Baroni Urbani & Kannowski 1974). *S. invicta* may remove >90% of bait in less than 2 h. Furthermore, hydramethylnon decomposes rapidly with exposure to sunlight (Vander Meer et al. 1982) and leaves no detectable residues after 24 h (Apperson et al. 1984). We conclude that fire ants negatively affected overall insect biomass, richness, and diversity.

Shrike abundance was higher on sites where *S. invicta* populations were reduced. A mechanism responsible for lower shrike abundance on sites with higher fire ant populations may be the deterioration of habitat quality due to a decrease in the availability of insects. The better fit of non-linear models of the relationship between shrike abundance and fire ants suggests that there may be a threshold infestation level that occurs at fairly modest fire ant densities (Fig. 2). Food resource abundance affects territory quality, with sites supporting fewer insects also supporting lower densities of shrikes (Seki & Takano 1998). Shrikes largely feed on arthropods (Craig 1978) such as grasshoppers, crickets, and beetles (Lymn & Temple 1991). Red imported fire ants also feed heavily on arthropods (Hays & Hays 1959), and on our study sites we detected community-level negative effects on native insects. The indirect influence of *S. invicta* on insect availability also has been suggested as a mechanism of negative impact on quail populations (Allen et al. 1995). More direct resource co-option also may affect the quality of shrike habitat. Food caching behavior by the loggerhead shrike is not fully understood (Fraser & Luukkonen 1986), but does influence reproductive success

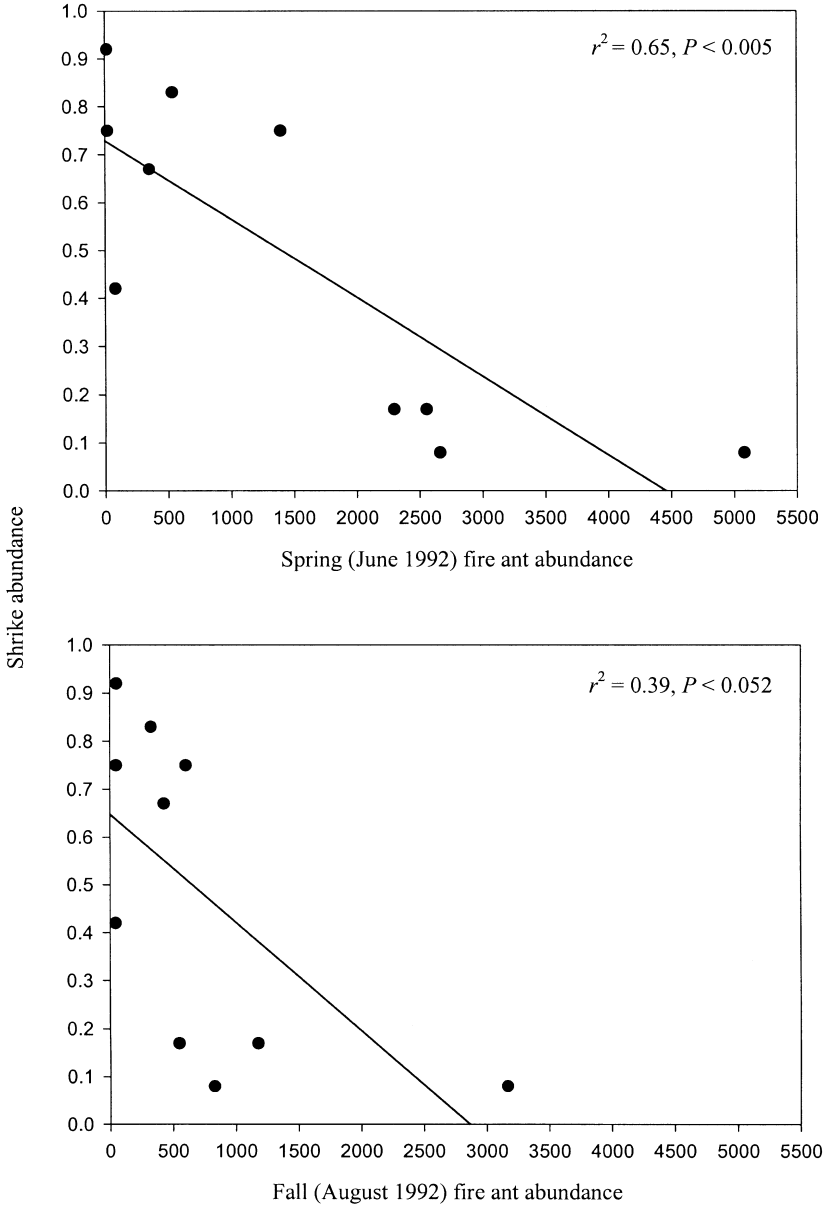

Fig. 1. Linear relationship between fall abundance of loggerhead shrikes and spring and fall fire ant abundance, 1992.

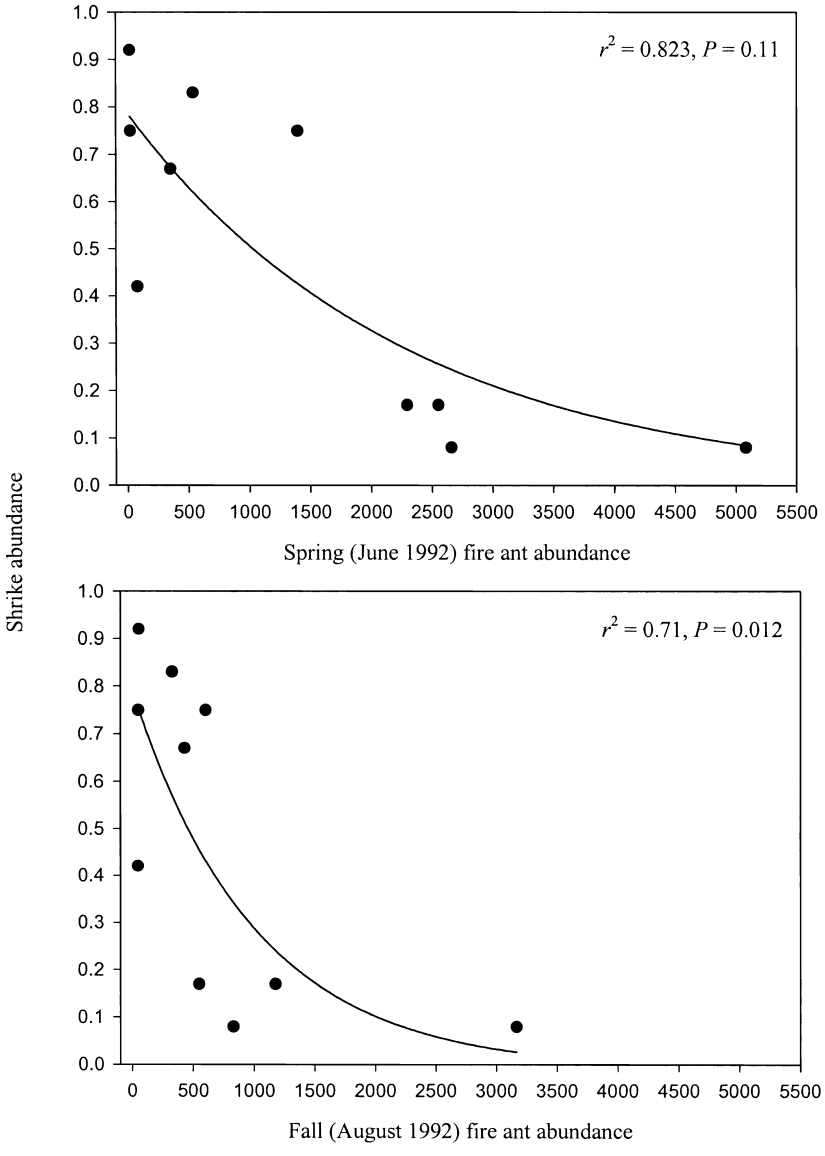

Fig. 2. Non-linear relationship between fall abundance of loggerhead shrikes and spring and fall fire ant abundance, 1992.

(Yosef & Pinshow 1989). In 1992, a loggerhead shrike was observed caching a freshly impaled grasshopper on a fence post and, minutes later, this grasshopper was dismembered and carried away by foraging *S. invicta* (C. R. A., personal observation). This observation and the speed of recruitment by *S. invicta* to food sources suggests that prey cached in areas heavily infested by *S. invicta* are likely

Table 4. Loggerhead shrike abundance (± one SE) on five pairs of treated and untreated study areas in the Texas Coastal Prairie >1 year after the cessation of treatments, 1 September–13 November 1993.

Study area pair	Treated	Untreated
R1	0.44 ± 0.13	0.42 ± 0.10
R2	0.29 ± 0.13	0.16 ± 0.09
V1	0.13 ± 0.09	0.07 ± 0.07
VC1	0.39 ± 0.14	0.75 ± 0.11
VC2	0.18 ± 0.10	0.05 ± 0.05
Mean ± SE	0.29 ± 0.06	0.29 ± 0.13

to be exploited by fire ants. If caching by male shrikes is important in the reproductive energetics (Applegate 1977) and success (Yosef & Pinshow 1989) of females, or as a reserve food source for shrikes in times of prey scarcity, this may be an additional mode of impact in the loggerhead shrike.

Conservation of native species often requires understanding the effect of invasive species upon native species, the mechanisms of impacts, and the factors leading to invasion. Predaceous invasive invertebrate species can have profound negative effects on native insect communities (Simberloff 1981), both by preying upon native species and by competing with them. The impact of *S. invicta* on native species diversity and abundance is becoming more clearly understood (Allen et al. 1998), yet more remains unknown than known concerning the ecological impacts of fire ants. However, it is clear that fire ants are a threat to native invertebrate and vertebrate communities, especially in areas where polygynous fire ants are established.

Acknowledgment

An earlier version of this manuscript was improved by comments from P. S. Allen and J. Zettler. We thank the J. F. Welder Heirs Ranch at Vidaurri, the McFaddin Ranch, and the P. H. Welder Ranch Green Lake Division for use of their properties. We thank American Cyanamid for their donation of fire ant bait, and H. Collins, Imported Fire Ant Station, USDA, APHIS, PPQ, for coordinating treatments. This research was funded in part by the state of Texas Fire Ant Line-Item for research. Approved for publication as Journal Article WF 155 of the Forest and Wildlife Research Center at Mississippi State University, manuscript T-4-520, Texas Tech University, College of Agricultural Sciences and Natural Resources, and contribution #571 of the Rob and Bessie Welder Wildlife Foundation. The South Carolina Cooperative Fish and Wildlife Research Unit is jointly supported by a cooperative agreement among the USGS/BRD, the South Carolina Department of Natural Resources, Clemson University, and the Wildlife Management Institute.

References Cited

Allen, C. R., S. Demarais & R. S. Lutz. 1994. Red imported fire ant impact on wildlife: an overview. Texas J. Sci. 46: 51–59.

Allen, C. R., R. S. Lutz & S. Demarais. 1995. Red imported fire ant impacts on Northern Bobwhite populations. Ecol. Appl. 5: 632–638.

Allen, C. R., R. S. Lutz & S. Demarais. 1998. Ecological effects of the invasive non-indigenous ant, *Solenopsis invicta*, on native vertebrates: the wheels on the bus. Trans. North Am. Wildl. Nat. Resour. Conf. 63: 56–65.

Allen, C. R., K. Rice, D. P. Wojcik & H. F. Percival. 1997. Effect of red imported fire ant envenomization on neonatal American alligators. J. Herpetol. 31: 318–321.

Apperson, C. S., R. B. Leidy & E. E. Powell. 1984. Effects of Amdro on the red imported fire ant (Hymenoptera: Formicidae) and some nontarget ant species and persistence of Amdro on a pasture habitat in North Carolina. J. Econ. Entomol. 77: 1012–1018.

Applegate, R. D. 1977. Possible ecological role of food caches of loggerhead shrike. Auk 94: 391–392.

Baroni Urbani, C. & P. B. Kannowski. 1974. Patterns in the red imported fire ant settlement of a Louisiana pasture: some demographic parameters, interspecific competition and food sharing. Environ. Entomol. 3: 755–760.

Bond, W. & P. Slingsby. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. Ecology 65: 1031–1037.

Cokendolpher, J. C. & S. A. Phillips Jr. 1989. Rate of spread of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae) in Texas. Southwest. Nat. 34: 443–449.

Cole, F. R., C. Guayasamin, O. Pazmino, C. Donoso & Y. Paez de Villacis. 1992. Effects of the Argentine ant on arthrodpod fauna of Hawaiian high-elevation shrubland. Ecology 73: 1313–1322.

Craig, R. B. 1978. An analysis of the predatory behavior of the loggerhead shrike. Auk 95: 221–234.

Drees, B. M. 1994. Red imported fire ant predation on nestlings of colonial waterbirds. Southwest. Entomol. 19: 355–359.

Fraser, J. D. & D. R. Luukkonen. 1986. The loggerhead shrike, pp. 933–941. *In* R. L. DiSilvestro [Ed.], Audubon wildlife report 1986. National Audubon Society, New York, 1000 pp.

Giuliano, W. M., C. R. Allen, R. S. Lutz & S. Demarais. 1996. Effects of red imported fire ants on northern bobwhite chicks. J. Wildl. Manage. 60: 309–313.

Glancey, B. M., C. H. Craig, C. E. Stringer & P. M. Bishop. 1973. Multiple fertile queens in colonies of the imported fire ant, *Solenopsis invicta*. J. Ga. Entomol. Soc. 8: 237–238.

Gould, F.W. 1975. The grasses of Texas. Texas A&M University Press, College Station, Texas, 664 pp.

Handel, S. N., S. B. Fisch & G. E. Schatz. 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. Bull. Torrey Bot. Club 108: 430–437.

Hays, S. B. & K. L. Hays. 1959. Food habits of *Solenopsis saevissima richteri* Forel. J. Econ. Entomol. 52: 445–447.

Lofgren, C. S. & D. F. Williams. 1982. Avermectin B^1a: highly potent inhibitor of reproduction by queens of the red imported fire ant (Hymenoptera: Formicidae). J. Econ. Entomol. 75: 798–803.

Lymn, N. & S. A. Temple. 1991. Land-use changes in the gulf coast region: links to declines in midwestern loggerhead shrike populations. Passenger Pigeon 53: 315–325.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, 179 pp.

Mirenda, J. T. & S. B. Vinson. 1982. Single and multiple queen colonies of imported fire ants in Texas. Southwest. Entomol. 7: 135–140.

Pedersen, E. K., W. E. Grant & M. T. Longnecker. 1996. Effects of red imported fire ants on newly hatched Northern Bobwhite. J. Wildl. Manage. 60: 164–169.

Porter, S. D. & D. A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71: 2095–2106.

Porter, S. D., A. Bhatkar, R. Mulder, S. B. Vinson & J. D. Clair. 1991. Distribution and density of polygyne fire ants (Hymenoptera: Formicidae) in Texas. J. Econ. Entomol. 84: 866–874.

Risch, S. J. & C. R. Carroll. 1982. Effect of a keystone predaceous ant, *Solenopsis geminata*, on arthropods in a tropical agroecosystem. Ecology 63: 1979–1983.

SAS Institute. 1989. SAS/STAT user's guide, version 6, 4th ed. SAS Institute, Cary, North Carolina, 1686 pp.

Seki, S. I. & H. Takano. 1998. Caterpillar abundance in the territory affects the breeding performance of great tit *Parus major minor*. Oecologia 114: 514–521.

Sikes, P. J. & K. A. Arnold. 1986. Red imported fire ant (*Solenopsis invicta*) predation on cliff swallow (*Hirundo pyrrhonata*) nestlings in east-central Texas. Southwest. Nat. 31: 105–106.

Simberloff, D. 1981. Community effects of introduced species, pp 53–81. *In* M. H. Nitecki [Ed.], Biotic crisis in ecological and evolutionary time. Academic Press, New York, 301 pp.

Tacha, T. C., W. D. Wade & K. P. Burnham. 1982. Use and interpretation of statistics in wildlife journals. Wildl. Soc. Bull. 10: 355–362.

Vander Meer, R. K., D. F. Williams & C. S. Lofgren. 1982. Degradation of the toxicant AC 217,300 in Amdro imported fire ant bait under field conditions. J. Agric. Food Chem. 30: 1045–1048.

Vinson, S. B. & A. A. Sorensen. 1986. Imported fire ants: life history and impact. Texas Department of Agriculture, Austin, Texas.

Wojcik, D. P. 1983. Comparison of the ecology of red imported fire ants in North and South America. Florida Entomol. 66: 101–111.

Wojcik, D. P. 1994. Impact of the red imported fire ant on native ant species in Florida, pp. 269–281. *In* D. F. Williams [Ed.], Exotic ants: biology, impact, and control of introduced species. Westview Press, Boulder, Colorado, 332 pp.

Yosef, R. & B. Pinshow. 1989. Cache size in shrikes influences female mate choice and reproductive success. Auk 106: 418–421.

Zettler, J. A., T. P. Spira & C. R. Allen. 2001. Ant-seed mutualisms: can fire ants sour the relationship? Biol. Conserv. 101: 249–253.